THE GENUS ODONTITES (SCROPHULARIACEAE) IN NORTHWEST EUROPE

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LUND 1983

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Fil mag Hb

AKADEMISK AVHANDLING

som för avläggande av filosofie doktorsexamen vid Matematisk-Naturvetenskapliga fakulteten vid Universitetet i Lund kommer att offentligen försvaras å föreläsningssalen vid Institutionen för systematisk botanik, fredagen den 2 dec. 1983 klockan 10.00.

Lund 1983

Organization
LUND UNIVERSITY
Department of Systematic Botany
Ö. Vallgatan 18-20
S-223 61 Lund, Sweden

Document name
DOCTORAL DISSERTATION

Date of issue
December 2, 1983

CODEN:
LUNDBDS/NBBS-1007/1-95 (1983)

Author(s)
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Sponsoring organization

Title and subtitle

The genus Odontites (Scrophulariaceae) in northwest Europe.

Abstract The NW European taxa of Odontites have been taxonomically revised. The following taxa are accepted: O. verna (Bellardi)Dum. (2n=40), O. vulgaris Moench (2n=18), O. litoralis (Fries) Fries subsp. litoralis (2n=18) and O. litoralis subsp. fennica Markl. (2n=18). A key, descriptions, nomenclature, illustrations and distribution maps are provided. Field observations on variation, frequency, pollination biology, ecology and associated species were made in 123 populations. Lists of associated species are given. Cultivation experiments under uniform conditions were carried out with 31 populations using Trifolium repens as host species, and with 5 selected populations on 12 different host species and autotrophically. Survival, onset of flowering, plant height, inflorescence length, number of branches and dry weight differed with the host plant. Morphological variation within and between populations and between taxa with reference to both wild and cultivated material was comprehensively analysed. Crossing experiments were performed within and between populations and between taxa. O. verna was found to be totally incompatible with the other taxa. Fertile hybrids between O. litoralis and O. vulgaris were produced but a considerable F_2 breakdown occurred. The isolation between O. litoralis and O. vulgaris is maintained by the combined effects of difference in flowering time, difference in habitat preference, the predominance of self-pollination in O. litoralis and the breakdown of vitality in hybrid swarms. The two subspecies of O. litoralis are geographically isolated. Populations intermediate between the subspecies have been found.

Key words Scrophulariaceae, Odontites, taxonomy, nomenclature, hemiparasites, host - parasite relationship, crossing experiments

Classification system and/or index terms (if any)

Supplementary bibliographical information

Language Englis

ISSN and key title

ISBN

Recipient's notes

Number of pages 95

Price

Security classification

Distribution by (name and address) Britt Snogerup, University of Lund, Department of Systema
Botany, Ö. Vallgatan 18, S-223 61 Lund, Sweden

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DOKUMENTDATABLAD enl SIS 61 41 21

UNIV. LEIDEN BIBL.

PREFACE

This thesis summarizes investigations on the northwest European taxa of *Odontites* made during the period 1975-81 in natural populations in Denmark, Sweden and S Finland and in cultivation together with a study of all available herbarium material of the taxa from the following herbaria (abbreviations according to Holmgren et al. 1981): BG, BM, BR, C, GB, H, K, LD, LINN, O, OULU, S, TRH, TROM, TUR, UME, UPS, UPSV and of selected material from CL, JE, MW and OXF. Central to the study has been a crossing programme, biometrical investigations on the material cultivated under uniform conditions and the cultivation of some selected populations on different host species.

The thesis is based on the following publications which are referred to by Roman numerals:

I Snogerup, B. 1977: Chromosome numbers of Scandinavian Odontites species. - Bot. Notiser 130: 121-124.

II Snogerup, B. 1982: Odontites litoralis subsp. litoralis in the British Isles. - Watsonia 14: 35-39.

III Snogerup, B. 1982: Host influence on northwest European taxa of Odontites (Scrophulariaceae). - Ann. Bot. Fennici 19: 17-30.

IV Snogerup, B. 1983: Northwest European taxa of Odontites (Scrophulariaceae). - Acta Bot. Fennica 124: 1-62.

INTRODUCTION

The genus *Odontites* is represented by the following taxa in NW Europe: *O. verna* (Bellardi) Dumortier, *O. vulgaris* Moench, *O. litoralis* (Fries) Fries subsp. *litoralis* and *O. litoralis* subsp. *fennica* Marklund.

The taxonomic treatment of the taxa has varied with different authors. The names *O. verna* and *O. rubra* have both been used in a collective sense. Linneaus (1753) treated the northwest European taxa under the name of *Euphrasia odontites*. *Euphrasia verna* was described by Bellardi (1788) as a species distinct from *E. odontites* and was correctly combined under *Odontites* by Dumortier (1827). *O. vulgaris* was proposed as a new name for *E. odontites* by Moench (1794) but little attention was paid to this name for nearly two hundred years. Instead, the illegitimate names *O. rubra* and *O. serotina* were used for this taxon. Fries (1835) described *E. odontites* var. *litoralis* and in 1845 gave it species rank. Marklund (1955) distinguished *O. litoralis* subsp. *fennica* from the Gulf

of Finland. Within *O. vulgaris* the following infraspecific taxa, not accepted here, have been proposed in works dealing with the group from this area: subsp. *pumila* by Pedersen (1963) for some coastal ecotypes, subsp. *rothmaleri* by Schneider (1965) for plants from man-made inland habitats, f. *tescaria* by Johansson (1897) for tiny alvar specimens and β *pallida* by Lange (1851) for pale-flowered specimens.

SURVEY OF THE TAXA

Table 1 gives a survey of some important characters of the taxa.

O. verna is a tetraploid (2n=40), fairly early-flowering weed, of ryefields in particular. The general distribution of *O. verna* is the whole of Europe except the extreme north and the Mediterranean, and W Asia. The distribution in Denmark, Sweden, Norway and Finland is shown in IV, Fig. 2.

O. verna has diminished in frequency during the last thirty years but is still fairly common. The reduction is evidently connected with changes in the mode of cultivation which includes the use of herbicides and fertilizers. *O. verna* seems to be dependent on the fairly continuous cultivation of rye in the same or neighbouring fields but it is not host-specific to rye (III). It is probably rather the light requirements and the preference for light sandy soils, where rye is often cultivated, that influence the occurrence of *O. verna*.

O. vulgaris is a diploid (2n=18), summer- to autumn-flowering, occurring in salt and brackish marshes and in man-made habitats. The general distribution of *O. vulgaris* is the whole of Europe except the extreme north, and temperate Asia to China. It is introduced in N America. The distribution in Denmark, Sweden, Norway and Finland is shown in IV, Fig. 4.

O. vulgaris has the widest habitat preference of the NW European *Odontites*. It is very common in the *Festuca rubra* zone of salt and brackish marshes and in inland localities that are the result of human activity e.g. grazed meadows and pastures. *O. vulgaris* also occurs on the alvar areas of Öland and Gotland and as a weed on arable land and in open man-made habitats such as roadsides, gravel pits and abandoned fields. It is not so sensitive to grazing as *O. litoralis* subsp. *litoralis* since it is more disposed to branch. If the terminal inflorescence is grazed flowering branches will grow out lower down thus guaranteeing seed set.

TABLE 1. COMPARISON OF SOME CHARACTERS OF NORTHWEST EUROPEAN TAXA OF ODONTITES

Character	*O. verna*	*O. vulgaris*	*O. litoralis* subsp. *litoralis*	*O. litoralis* subsp. *fennica*
Stem	10-25 cm	15-50 cm	5-20 cm	18-50 cm
Branches	1-4 pairs, short, erect, in the upper part of the plant (sometimes from the base)	1-8 pairs, long. ± patent to suberect, from the base or higher up	usually simple, 1-3 pairs, short	0-6 pairs, long, erect, lowest branch at node 5-7
Angle between stem and branches	30-50°	50-85°	c. 30°	20-40°
Leaves	Longer than internodes, very narrowly ovate to almost linear, widest close to the base, thin	Longer than internodes, very narrowly ovate, widest 1/4-1/3 from the base, thin (weeds) or thick (seashore plants)	Shorter than or as long as internodes, narrowly ovate, with rounded apex, thick	Longer than internodes, very narrowly ovate, with rounded apex, thick
No. of intercalary leaves'	0. rarely 1 pair	3-7 pairs	0, rarely 1 pair	0, rarely 1-2 pairs
Inflorescence	Short, compact, many-flowered	Long, lax, many-flowered	Short, rather lax, few-flowered	Long, lax, many-flowered
Lowest flower at node number	6-9	8-14	4-8	6-12
Bracts	Exceeding flower	Usually not exceeding flower	Equalling or exceeding flower	Exceeding flower
Style at the completion of anthesis	Exceeding upper lip	Exceeding upper lip	Not exceeding upper lip	Not exceeding upper lip
Calyx	Teeth narrow, acute, as long as tube	Teeth narrow, acute (weeds) or triangular, obtuse (seashore plants), shorter than tube	Enlarges while capsule ripens. Teeth triangular, obtuse, shorter than tube	Enlarges while capsule ripens. Teeth triangular, obtuse, shorter than tube
Capsule	Equalling calyx	Equalling (weeds) or exceeding (seashore plants) calyx	Exceeding calyx	Exceeding calyx
Flowering period	15.6-30.7	10.7-30.9	15.6-30.7	10.7-15.8
Habitat	Arable land, preferably ryefields	Fields, roadsides, pastures, meadows, salt marshes	Salt and brackish marshes, gravelly and rocky seashores	Brackish marshes, gravelly and rocky seashores
2n	40	18	18	18

'= Leaves on the main stem without flowers in their axils, immediately above the uppermost branches.

O. litoralis subsp. *litoralis* is an early-flowering diploid (2n=18) growing in salt and brackish marshes from the Netherlands to S Norway, in the northern part of the British Isles and along the shores of the Baltic. The distribution in the British Isles is given in II, Fig. 1, in the Netherlands in Adema (1980) and the rest of the total distribution in IV, Fig. 6.

O. litoralis subsp. *litoralis* inhabits the outer zone of salt and brackish marshes and is in most localities restricted to the plant community dominated by *Juncus gerardi*. It is very sensitive to early grazing as it is less disposed to branch than *O. vulgaris*. Early grazing can prevent *O. litoralis* subsp. *litoralis* from setting seed thus rapidly leading to extinction.

O. litoralis subsp. *fennica* (2n=18) is slightly more late-flowering than subsp. *litoralis*. It is almost entirely restricted to the Gulf of Finland but is also found on the SE coast of the Gulf of Bothnia (IV, Fig. 8). Subsp. *fennica* inhabits the litteral zone and is found in different types of more or less open vegetation in gravelly, sandy or rocky habitats. It is often commonest near the drift-line and among washed-up seaweed.

CULTIVATION EXPERIMENTS

Seeds collected in the field or harvested in cultivation were stored indoors at room temperature until they were sown in November or December. The seeds were sown in pots placed in peat in open frames and were left outdoors during the winter to break dormancy. The *Odontites* seeds need 12-18 weeks of low winter temperature and moisture to germinate (Vallance 1951). Experiments with seeds that have been stored in a refrigerator or a deep-freeze and sown on filter paper were not successful. The seeds became mouldy and did not germinate. Rottgardt (1956) had the same experience.

Nearly all attempts to transplant the seedlings failed. Instead a few seeds were sown in each of those pots where the plants were intended to grow. In spring when the *Odontites* had germinated seeds of the host plant were sown in the same pots.

The northwest European species of *Odontites* are annual hemiparasites. They have functional chlorophyll but obtain water, minerals and organic compounds from their hosts through haustorial root connections. They are able to live autotrophically but then produce only a few flowers and seeds. The *Odontites* taxa are not host-specific; a great many angiosperms can function as hosts (Govier et al. 1967, Weber 1976 and III) although with varying results. Cultivation on different hosts showed that habit, plant height, inflorescence length, number of branches and dry weight varied with the host (III). The *Odontites* plants did not do well with all species they were tested with. When grown with *Plantago lanceolata* and *Triglochin maritima* all *Odontites* seedlings died and with *Festuca rubra* and *Carex distans* there were pronounced differences in survival between the different *Odontites* taxa.

Variation between populations and taxa was analysed on material cultivated under uniform conditions, using one and the same host for

all viz. *Trifolium repens*. Characters used by previous authors together with other putative key characters were investigated in detail and measurements were treated statistically (IV).

It is often impossible to determine *Odontites* specimens on a single character. If as many characters as possible and several individuals from a population are considered together there is generally no difficulty in identifying the material as the taxa recognized here by means of the characters given in Table 1.

CROSSING EXPERIMENTS

To investigate whether there are any sterility barriers between taxa or populations I designed a crossing programme along the following lines: self-pollination, pollination between individuals of the same population, pollination between individuals of different populations of the same taxon and pollination between individuals of different taxa (IV).

Parental material

For comparison with the results obtained in crosses, seed set obtained after open pollination both in wild and cultivated material, germination of seeds collected in the field and pollen stainability were determined for the parental material.

Seed set was higher in *O.litoralis* than in *O. verna* and *O. vulgaris* in both wild and cultivated material which may be a result of the predominance of self-pollination in *O. litoralis*. Germination was highest for seeds of *O. litoralis* subsp. *fennica* and lowest for those of *O. verna*. In all taxa some plants showed a reduction in pollen stainability. The highest value was obtained for *O. litoralis* subsp. *fennica*, 95% of the plants having more than 90% good pollen. In the other three taxa 67-80% of the plants had more than 90% good pollen.

Selfings

Flowers of all taxa were isolated and allowed to self spontaneously. Those of *O. litoralis* set seed spontaneously but flowers of *O. vulgaris* and *O. verna* had to be artificially selfed. *O. verna* had the lowest seed set and *O. litoralis* subsp. *litoralis* the highest. In the two subspecies of *O. litoralis* germination was higher in seeds obtained by selfing than

in seeds collected in the field; in *O. vulgaris* seeds from self-pollination showed the same germination rate as those harvested in nature. After selfing germination in *O. verna* was remarkably low (4% as compared with 29% for spontaneous seeds).

Crosses within populations

In *O. litoralis* subsp. *litoralis* and *O. vulgaris* the average seed set obtained in intrapopulation crosses was nearly the same as after selfing but lower than that obtained after open pollination. In *O. litoralis* subsp. *fennica* and *O. verna* it was twice as high as after selfing and showed nearly the same value as in parental material after open pollination. The germination of the seeds obtained in intrapopulation crosses was even higher than that of seeds collected in the field. Pollen stainability of the F_1 plants was more than 90%.

Crosses between populations

For interpopulation crosses within *O. litoralis* subsp. *litoralis* and *O. vulgaris* seed set varied within roughly the same range independent of the geographical distance between the parental populations. The populations of *O. litoralis* subsp. *fennica* used in crosses are all situated less than 10 km apart. The mean seed set was for this taxon lower in interpopulation crosses than in intrapopulation crosses possibly due to reciprocal differences between the populations. In *O. verna* the highest and lowest values for seed set were obtained in crosses between populations situated close together, in crosses between populations situated farther apart the values were intermediate and almost the same as in intrapopulation crosses.

For *O. verna* germination was nearly the same in both intra- and interpopulation crosses, for *O. litoralis* subsp. *litoralis* it was higher in intrapopulation crosses and for *O. litoralis* subsp. *fennica* it was higher in interpopulation crosses. No seeds of *O. vulgaris* from intrapopulation crosses were sown, so no comparison could be done between the two levels for this species.

Most F_1 plants were fully vital but pollen stainability was lower than in the parental material and in intrapopulation crosses. Pollen stainability was especially low in some crosses between those populations

of *O. litoralis* subsp. *litoralis* that were farthest apart. In these F_1 families no seeds were obtained after selfing. Seed set after selfing was also low in the other F_1 families, far lower than after cross-pollination and after selfing in the parents. A great number of the isolated F_1 flowers failed to set at all.

Seeds from F_1 plants of *O. vulgaris* had a higher rate of germination than those obtained in interpopulation crosses, those of *O. litoralis* a somewhat lower one. Only the F_1 seeds of *O. verna* had a much lower germination although it was not as low as that obtained after selfing in the parents.

Most F_2 plants were fully vital in the meaning that they flowered and set seed, but they varied considerably in size and F_2 segregations occurred in some families. Nearly all F_2 plants of *O. vulgaris* were more vigorous and taller than the F_1 plants; in *O. litoralis* subsp. *fennica* and *O. verna* the F_2 plants were much smaller than the F_1 plants. Pollen stainability was restored in F_2.

Crosses between taxa

O. litoralis subsp. *litoralis* x subsp. *fennica*

The mean seed set in crosses between the two subspecies of *O. litoralis* was about half that of interpopulation crosses within the parents. Germination was, however, higher in the hybrid seeds than in the seeds of both taxa produced in nature.

The F_1 plants were fully vital, resembling in size and habit subsp. *fennica*, but were intermediate between the parents in some characters. Pollen stainability was lower in the F_1 plants than in the parents and seed set was much lower after selfing in the F_1 flowers than in crosses between the parents. Seeds from F_1 plants had almost the same germination rate as the spontaneous seeds of the parents. There was a conspicuous F_2 segregation but pollen stainability was restored.

O. litoralis x *O. vulgaris*

9 of the 10 attempts to cross *O. litoralis* and *O. vulgaris* were successful. The mean seed set was lower than in interpopulation crosses within *O. litoralis*, but nearly the same as in interpopulation crosses within *O. vulgaris*. A high percentage of the hybrid seeds germinated.

Most of the F_1 hybrids were fully vital and were intermediate between the parents in general appearence. Pollen stainability in the F_1 hybrids was on the whole somewhat lower than in the parents but slightly higher than in the F_1 plants of interpopulation crosses within the parents. Selfing in one F_1 family failed completely, in the others seed set was obtained in c. 25% of the isolated flowers. Mean seed set and germination of the seeds from F_1 plants were intermediate to what was found in the interpopulation crosses within the parents. An F_2 segregation including different abnormalities occurred in all families. Pollen stainability was partially restored in the F_2 plants.

Between *O. verna* and the other taxa

A great number of attempts were made to cross the tetraploid *O. verna* with the diploid taxa. Seed set was obtained in 4 crosses only, the total number of mature seeds being 5. None of the seeds germinated.

CYTOLOGY

The chromosome number was determined for all populations used in crossing experiments. In *O. vulgaris* and *O. litoralis* the chromosome complement consist of 18 and in *O. verna* of 40 metacentric to submetacentric chromosomes (I). The chromosomes gradually decrease in size from 3.5 µm to 1 µm. A satellite was often observed on one of the longest pairs. A few plants had aneuploid numbers.

Meiosis was examined in some of the parents and was found to be normal. In *O. vulgaris* and *O. litoralis* one bivalent usually divides precociously giving the impression that there are 10 bivalents instead of 9. In the F_1 families most observations were made at diakinesis, metaphase I and metaphase II (IV). Irregularities were rare and no more occurred in the interspecific crosses than in interpopulation crosses.

It was only possible to study pollen mitosis in the parental material of *O. verna*.

GENERAL CONCLUSIONS

(1) There are strong incompatibility barriers between tetraploid *O. verna* and the two diploid species *O. litoralis* and *O. vulgaris*. There is probably no gene exchange between *O. verna* and the other species.
(2) The incompatibility barriers between *O. litoralis* and *O. vulgaris* are weaker than those between the tetraploid and the diploids. The isolation between the two diploid species is maintained by the combined effects of difference in flowering time, difference in habitat preference, the predominance of self-pollination in *O. litoralis* and the breakdown of vitality in hybrid swarms.
(3) The incompatibility barriers between *O. litoralis* subsp. *litoralis* and *O. litoralis* subsp. *fennica* are no stronger than those existing between some populations of subsp. *litoralis*. The isolation between the two subspecies is geographical, and ecological differences are therefore currently of no importance.
(4) Selfing is commoner in *O. litoralis* than in *O. verna* and *O. vulgaris*.
(5) The general appearance of the *Odontites* plants depends to some extent on what host is parasitized - plant height, number of branches, inflorescence length, mode of branching and onset of flowering are modified by the host.

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Tryckericentralen
AVC Lund 1983